Bryophyte Floras of Four Acid-Sensitive Lakes in South-central Ontario: Description and Mechanisms of *Sphagnum* invasion

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Table of Contents

	Page
List of Tables	ii
List of Figures	iii
Introduction	1
Description of the Study Area	2
Methods	2
Results and Discussion	4
Bryophyte Occurrence	4
Analysis of Cores	4
Acknowledgements	8
References	9

List of Tables

Table 1 Selected geographic, morphometric and chemical data from the study lakes, the last from Dillon (unpubl. data). Bryophyte species reported by Wile and Miller (1983) are indicated.

Table 2 Distribution of aquatic and semiaquatic bryophytes in the study lakes. Numeric codes indicate occurrence at or in lake edges (1), inlet fens, bogs or moats (2), surface of lake sediments (3), upland bogs (4), forest soil depressions (5), and lake outlets (6).

Table 3 Occurrence of terrestrial bryophytes in watersheds of the study lakes.

List of Figures

Figures 1-4 Bathymetric maps (depths in m) of Crosson, Gullfeather, Plastic and Moot Lakes, respectively. The closed circle indicates the sediment coring location, the squares, areas of *Sphagnum* occurrence, the diamonds areas of *Fontinalis* occurrence.

Figures 5-8 Distribution of pollen spores and bryophyte spores and gametophyte fragments in sediment cores of Crosson, Gullfeather, Moot and Plastic Lakes, respectively. A) Relative abundance of the sum of pollen grains of major upland taxa (%). B) Relative abundance of native terrestrial cryptogam spores and algae (% of upland pollen total). C) Concentration (numbers X 10^3/g dry weight of sediment) of pollen, spores, algae and bryophyte gametophyte fragments. Only in Crosson Lake were gametophyte fragments quantitatively important for taxa other than *Sphagnum*.

Introduction

In Europe, one frequently reported consequence of acidification of softwater lakes is a replacement of vascular macrophytes (tracheophytes) by extensive beds of the bryophyte Sphagnum (Grahn 1977, Eriksson et al. 1983, Roelofs 1983). In North America, Sphagnum invasions have been reported in Colden Lake (Hendrey and Vertucci 1980) and in 2 of 5 other acidic lakes (Roberts et al. 1985) in the Adirondack Mountains of New York, and in Little Springfield Lake in Nova Scotia (Kerekes et al. 1984). In a survey of the macrophytes, principally the vascular macrophytes of 46 lakes in Ontario ranging in pH from 3.3 to 7.0, Wile and Miller (1983) observed Sphagnum in 22 lakes ranging in pH from 4.0 to 7.0. Extensive growths were observed in only a few lakes, however, and there was little evidence that Sphagnum had expanded at the expense of the typical tracheophyte flora of non-acidic, softwater lakes. Excepting Wile and Miller's survey, no detailed information on the occurrence and composition of aquatic bryophyte floras exists for lakes in Ontario that are sensitive to acid deposition. Because of the reported frequency of extensive Sphagnum growth in acidified lakes in other areas, a detailed study of the aquatic bryophytes, Sphagnum in particular, of Precambrian Shield lakes of low alkalinity in Ontario was warranted.

Personnel of the Ontario Ministry of the Environment have been studying numerous lakes in the vicinity of Dorset, Ontario, since 1975. The occurrence of aquatic, semiaquatic and terrestrial bryophytes in the waters and drainage basins of 4 of these lakes (Moot, Plastic, Gullfeather and Crosson) is reported herein. In addition to documenting the presence and distribution of bryophytes, the potential significance of anthropogenic activities to bryophyte colonization of these lakes is considered by correlating the abundance of bryophyte propagules (spores and gametophyte fragments) in cores of lake sediments with palynological markers for the settlement of southern Ontario during historic time. The markers used are the decline in relative abundance of tree, principally hardwood, pollens and the increase in the relative abundance of ragweed pollen (Boyko 1973, Karrow and Anderson 1975).

Description of the Study Area

The four lakes are located in the Georgian Bay section of the Great Lakes-St. Lawrence forest region (Rowe 1972), an area that was extensively logged about 100 years ago. Watershed soils are sandy acidic podzols or brunisols with inherently low acid neutralizing capacity. Sugar maple, beech, basswood, yellow birch, eastern hemlock, eastern white pine, red maple, and white ash are the dominant trees in the region. Jack pine, red oak, large-toothed aspen, and trembling aspen also occur (Rowe 1972).

The locations of the lakes are given in Table 1. Bathymetric maps are sketched in Figures 1 to 4 and presented in Nicolls et al. (1983) in detail. The lakes are all small and Plastic and Gullfeather Lakes have undeveloped shorelines and watersheds. There are several cottages on the shores of Moot Lake and a camp on the shores of Crosson Lake, but these should not exert a large influence on the bryophyte flora. In terms of watershed position, Plastic and Moot are first order (headwater) lakes and Crosson and Gullfeather are second order lakes.

The pH levels (average for the ice-free season) of the lakes ranged from 5.78 in Crosson Lake to 5.99 in Gullfeather Lake in 1980 (Table 1). While precipitation in the area is very acidic (pH-4.1, Dillon et al. 1978) and ephemeral reductions in surface water pH associated with springmelt have been observed (Jeffries et al. 1979), the coloured waters of Moot Lake indicate that its low pH is probably attributable to organic acids. In contrast, the high clarity of Plastic Lake indicates that the low pH of this lake may be primarily attributable to the atmospheric deposition of strong acids.

Species of aquatic bryophytes previously recorded in the lakes by Wile and Miller (1983) are indicated in Table 1. Wile and Miller reported occurrence in nearshore and offshore areas; hence, only species that were submerged during the surveys were recorded.

Methods

In the autumn of 1980, bryophyte surveys were conducted around the entire shore of each lake. Particular attention was directed to upland forest soil depressions, to inflows and outflows of each lake

and to any extensive areas of bog around each lake. Specimens were collected and identified using herbarium collections at the University of Toronto and the keys and checklists of Shuster (1949), Crum (1973), and Ireland and Cain (1975).

In February or March of 1981, a sediment core, 50-130 cm in length, was taken through the ice in each lake with a modified Livingstone sampler (Rowley and Dahl 1956) at a single location where the water depth was about 4m (Figures 1-4). This depth was chosen in part because of the shallowness of Moot Lake, and because it approximated euphotic zone depth in the coloured lakes. Three subsamples were taken at 10 cm intervals along the length of the core for analysis of water, organic carbon and carbonate content, for bryophyte gametophyte fragment and spore analyses and for higher plant pollen analyses, respectively.

Samples were prepared for pollen analysis using the methods of Faegri and Iversen (1975) i.e. KOH, acetolysis, staining, dehydration and mounting in silicon oil. Pollen and native spores were identified using the reference collection at the Royal Ontario Museum, and the keys of McAndrews et al. (1973) and Boros and Jarai-Komlodi (1975). About 300 pollen grains of common upland plants were counted in each pollen subsample to locate the stratigraphic position of the Ambrosia (ragweed) horizon, the depth considered to demarcate the human settlement horizon.

To aid in determination of total pollen density, a known quantity of spores (usually 23,700) of the club moss Lycopodium clavatum was mixed into each core fraction prior to enumeration (Stockmarr 1970). These spores are referenced as 'exotic' as opposed to 'native' cryptogam spores. While 300 pollen grains of common upland taxa were counted, the count of pollen of aquatic species, of algae and of pollen of rare upland taxa was continued until 100 exotic spores were encountered. Cryptogam spore abundance was reported as a percentage of the pollen grain total - a count which excluded these spores.

Dinoflagellate cysts and remains of algae other than diatoms were also counted. Macroscopic plant fragments were separated from sediment on a 150 µm mesh screen and counted.

The spore, pollen or plant fragment concentrations (numbers/gram dry weight of sediment) were calculated by a modification of the technique of Davis (1966). Assuming a homogeneous distribution of exotic spores in sediment samples, the amount of sediment examined (S_o) was calculated from the number of exotic Lycopodium spores observed (L_o) knowing the number initially added (L_i) to a known sediment weight (S_i) as $S_o = S_i \cdot L_o / L_i$. For example, if 10^5 spores were added to 1 g of sediment, and the count terminated when 100 of these spores were encountered, a calculated total of 1 mg of sediment was actually examined.

Results and Discussion

Bryophyte Occurrence

Bryophytes were observed at many locations at or just above the water line of the lakes, in and along the edges of inlet and outlet streams, and submerged in the lakes (Tables 2 and 3). Sphagnum and other bryophyte taxa occurred around the shores of all four lakes (Figures 1-4), but only Plastic and Moot Lakes had extensive developments of peat. A total of nine Sphagnum species and nine other aquatic and semiaquatic bryophyte species were observed (Table 2). As 6 and 5 Sphagnum spp. were noted in and around the shores of Crosson and Moot Lakes, respectively, while Wile and Miller (1983) did not record the presence of Sphagnum in these lakes, it is probable that seasonally submerged Sphagnum is present in and around far more Shield lakes than would be concluded from Wile and Miller's survey. This indicates that a potential 'inoculum' for Sphagnum may exist in most Precambrian Shield lakes that are sensitive to acid input.

Analysis of Cores

One general feature of pollen diagrams of sediment cores of lakes from the mixed forest region of Ontario is the occurrence of a zone characterized by the decline in relative abundance of pollen of forest taxa and the increased prominence of pollen of herbaceous plants, notably ragweed (Ambrosia). This zone has been correlated with land clearance and the onset of European style agriculture, and dated

at about 1820 from sediment cores from Crawford Lake in southern Ontario (Boyko 1973, McAndrews 1981). This zone begins at a core depth of 15-20 cm in Crosson Lake, 30-35 cm in Gullfeather Lake and 25-30 cm in Moot Lake (Figures 5-7). The exact date of the beginning of this horizon has not been determined for lakes on the Canadian Shield. The first evidence of modern forestry practices on the Shield is from mills established at the northern end of Lake Simcoe in 1850. Logging activity increased in the Muskoka-Haliburton area by about 1860. This indicates that in the study area, the Ambrosia pollen zone, hereafter called the settlement horizon, spans the period from about 120 years ago to the present.

At the beginning of this zone there is a decline in the relative abundance of hemlock and beech pollen, possibly reflecting selective cutting of hemlock for tanneries and beech for hardwood. A later rise in the abundance of pine, birch and maple pollen (Figures 5 and 6), may indicate secondary forest growth after the decline of the logging industry between 1910 and 1930.

Pollen deposition was continuous throughout the length of the cores from Crosson, Gullfeather and Moot Lakes (Figures 5-7). The Crosson Lake core has a mid-Holocene decline in hemlock, the onset of which has been dated at approximately 4800 BP (before present). This feature is not apparent in the cores from the other lakes because of their shorter lengths. Other than the settlement zone, features evident in those cores are: 1) a decline in recent sediment in the relative abundance of the fern Osmunda, and 2) a recent increase in the common (K. Nicholls, pers. comm.) dinoflagellate, Peridinium wisconsinense. Peaks of gametophyte fragments of bryophytes, Sphagnum in particular, occurred at the onset of the settlement horizon. This is probably attributable to erosion of shoreline vegetation after forest clearing.

Sphagnum spores and gametophyte fragments were present in cores from all the lakes (Figures 5-7). Gametophyte fragment densities were lower than spore densities by an amount that varied widely among depths in the core and among lakes. In Moot Lake, for example, the spore concentration was 20-300 times greater than the fragment concentration near the boundary of the settlement zone. In Gullfeather Lake the spore concentration was 50-1500 times the fragment concentration at that depth in the core. Densities of spores of other bryophytes

(Dicranum, Polytrichum, Aulocomnium and Hedwigia) did not change with depth in this lake. In Crosson Lake, Sphagnum spore concentrations were 30-170 times the fragment concentrations. In all cases a pronounced increase in the ratio of spores to gametophyte fragments occurs on or after the onset of settlement.

The water, organic carbon, $CaCO_3$ and pollen profiles in the cores of these three lakes suggested that water levels of the lakes had remained relatively uniform for 100s or, indeed, for 1000s of years. There were no major inexplicable discontinuities in the cores. This was not the case for Plastic Lake. The current water depth at the coring site in Plastic Lake is 4.8 m. The core was 50 cm long and was formed of a surface layer of gyttja (0-7.5 cm) on an intermediate layer of gravel (7.5-12 cm) and overlying a silty clay layer (>12 cm) deposited prior to 10,000 years BP.

Pollen analysis (Figure 8) revealed two gaps in the sedimentation record of Plastic Lake. The jack pine zone of the early Holocene (ca. 8000-10,000 years BP) and the mixed forest zone (ca. 7000 BP to the present) were virtually absent. While data from a single core must be interpreted with caution in this as in all the lakes, these observations suggest that water levels have probably fluctuated widely in Plastic Lake. As current water levels are controlled by the activities of beavers, this speculation does not seem unreasonable.

Examination of the core data and the distribution of Sphagnum around the lakes indicates that, in addition to normal aerial or fluvial transport of spores and gametophyte fragments, there are two mechanisms which could deliver large quantities of Sphagnum propagules which might speed the establishment of Sphagnum in Ontario Shield lakes. First, establishment could have followed increased erosion of marginal bogs following extensive logging about one century ago. The increased input of spores and gametophyte fragments of Sphagnum spp., Drepanocladus spp. and Aulacomnium to the lake basins might then have provided the propagules for vegetative regeneration. Although this inwash might have initiated moss carpets, it has not resulted in dense and widespread colonization in any of the four lakes except over portions of the lake margins. Secondly, invasions of Sphagnum could follow submergence of bogs attributable to elevations in lake level. Data from a single core indicate such a recent increase in lake level may have occurred in Plastic Lake.

Of course, lake levels may also fall, to the detriment of Sphagnum and other aquatic plants. Hitchin et al. (1984) noted extensive, heavy beds of Sphagnum at <1 m along one transect in Plastic Lake in 1979. Dale and Hartley (1985) repeated the survey in the summer of 1985 and found almost no Sphagnum. As the level of the lake fell by ~0.6 m in the fall of 1979 because the beaver dam at the outflow failed (L. Scott, pers. comm.), and as maximum Sphagnum cover was previously recorded at about this depth, the decrease in water level may have caused the decline in Sphagnum abundance.

For extensive beds of Sphagnum to develop in acidifying lakes in Ontario, environmental conditions would have to be suitable for Sphagnum growth and Sphagnum propagules would have to be present in sufficient quantity to allow colonization. Analyses of data from the cores of the 3 lakes with normal pollen stratigraphy indicates influx of one type of propagule (plant fragments) was at a maximum about a century ago. The presence of spores and fragments of Sphagnum throughout the cores indicate that such propagules are being continuously supplied to the lakes although at variable rates. As it is apparent that Sphagnum beds can grow very rapidly if conditions are suitable (Grahn 1977), we conclude that excepting Plastic Lake which had an extensive Sphagnum bed in one area in the initial survey, environmental conditions are not suitable for luxuriant Sphagnum growth in the study lakes. As Sphagnum propagules are probably continuously supplied to many sensitive Precambrian Shield lakes in central Ontario, it would be useful to identify those environmental conditions which would permit or encourage the proliferation of extensive Sphagnum beds. The recent work of Roelofs et al. (1984) indicates it might be profitable to begin such an investigation by examining lake and sediment pore water CO_2 levels in acidic lakes, and the CO_2 requirements of various Sphagnum species.

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Table 1: Selected geographic, morphometric and chemical data from the study lakes, the last from Dillon (unpub. data). Bryophyte species reported by Wile and Miller (1983) are indicated.

Parameter	Gullfeather	Crosson	Moot	Plastic
latitude	45°05'N	45°05'N	40°07'N	45°11'N
longitude	79°01'W	79°02'W	79°01'W	78°50'W
lake area (ha)	65.9	56.8	46.2	32.3
mean depth (m)	4.8	8.4	2.7	8.0
maximum depth (m)	13.0	25.0	7.9	16.0
pH*	5.99	5.78	5.82	5.79
TP (mg m^{-3})	14.0	12.1	30.6	7.4
colour (Hazen units)	22.0	11.9	111.0	5
Fontinalis antipyretica			X	
Fontinalis hypnoides var. *duriaei*		X		
Fontinalis sp.	X	X		X
Sphagnum subsecundum var. *contortum*	X			
Sphagnum subsecundum var. *platyphyllum*				X
Sphagnum sp.	X			

*Seasonal variability in pH levels may be substantial; hence, pH values in Wile and Miller (1983) diverge by up to 0.6 units from values presented here.

Table 2: Distribution of aquatic and semiaquatic bryophytes in the study lakes. Numeric codes indicate occurrence of or in lake edges (1), inlet fens, bogs or moats (2), surface of lake sediments (3), upland bogs (4), forest soil depressions (5) and lake outlets (6).

Species	Crosson	Gullfeather	Plastic	Moot
Sphagnum				
Section Palustria				
S. centrale	1	2	1	1
S. palustre		2		
Section Squarrosa				
S. squarrosom	1,5	1,5	1,5	1,5
Section Cuspidata				
S. cuspidatum	2			
Section Subsecunda				
S. subsecundum s.l.	1	1	1	1
Section Acutifolia				
S. fimbriatum	2	2	1	2
S. russowii	1	1	1	1
S. memoreum			6	
Section Rigida				
S. compactum			1	
Fontinalis hypnoides	3	3		
F. antipyretica		3		
Leptodictyum riparium	1,4		4	
Aulacomnium palustre	1	1	1	1
Drepanocladus uncinatus			1	1
D. revolvens	4		4	
Scapania nemorosa	1	1	1	1
Pellaea epiphylla	1	1	1	1
Pallivicinia lyallii	1	1	1	1

Table 3: Occurrence of terrestrial bryophytes in watersheds of the study lakes.

		Crosson	Gullfeather	Plastic	Moot
Sphagnaceae	Sphagnum girgensohnii	X	X		
	Sphagnum squarrosum	X	X	X	X
Ditrichaceae	Ditrichum pallidum	X			
	Ceratodon purpureus				X
Dicranaceae	Dicranella varia	X			
	Dicranum fuscescens			X	
	Dicranum scoparium	X	X	X	X
	Dicranum polysetum	X	X	X	X
	Dicranum viride	X	X	X	X
	Dicranum flagellare		X		
	Paraleucobryum elongatum	X	X	X	X
Leucobryaceae	Leucobryum glaucum	X	X	X	X
Grimmiaceae	Grimmia alpicola	X			
Bryaceae	Pohlia nutans	X	X	X	X
	Pohlia wahlenbergii	X			
Mniaceae	Plagiomnium cuspidatum	X	X	X	X
	Rhizomnium punctatum	X		X	
Aulacomniaceae	Aulacomnium palustre	X	X	X	X
Orthotrichaceae	Orthotrichum anomalum	X			
Hedwigiaceae	Hedwigia ciliata	X			
Thuidiaceae	Thuidium delicatulum	X	X	X	X
	Helodium blandowii		X		
Amblystegiaceae	Amblystegium serpens		X		
	Platydictya jungermanioides			X	X
Brachytheciaceae	Brachythecium acuminatum	X			
	Brachythecium reflexum		X		
Entodontaceae	Pleurozium shreberi	X	X	X	X
Hypnaceae	Callicladium haldanianum	X	X	X	X
	Hypnum imponens	X			
	Hypnum lindbergii	X	X	X	X
Hylocomiaceae	Hylocomnium spendens			X	
Diphysciaceae	Diphyscium foliosum				X
Tetraphidaceae	Tetraphis pellucida	X	X	X	X
Polytrichaceae	Atrichum undulatum	X	X	X	X
	Polytrichum commune	X	X	X	X
	Polytrichum juniperium	X	X	X	X
	Polytrichum piliferum	X	X	X	X
Marchantiales	Pellea epiphylla	X	X		
Matzgeriales	Pallivicinia lyallii	X	X		X
Jungermaniales	Barbilophozia barbata		X		
	Lophozia bicrenata				X
	Bazzania cf. hyalina				X
	Ptilidium pulcherimum				X

Figure 1

CROSSON LAKE

250m

Figure 2

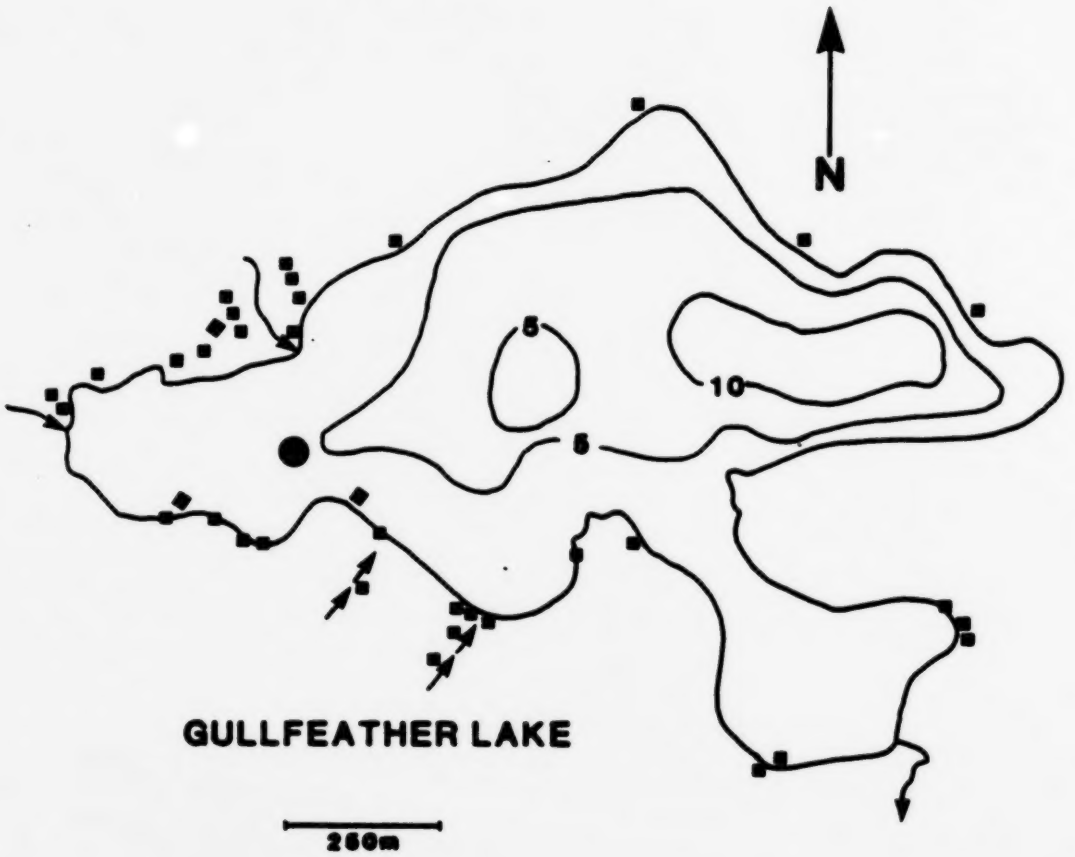

Figure 3

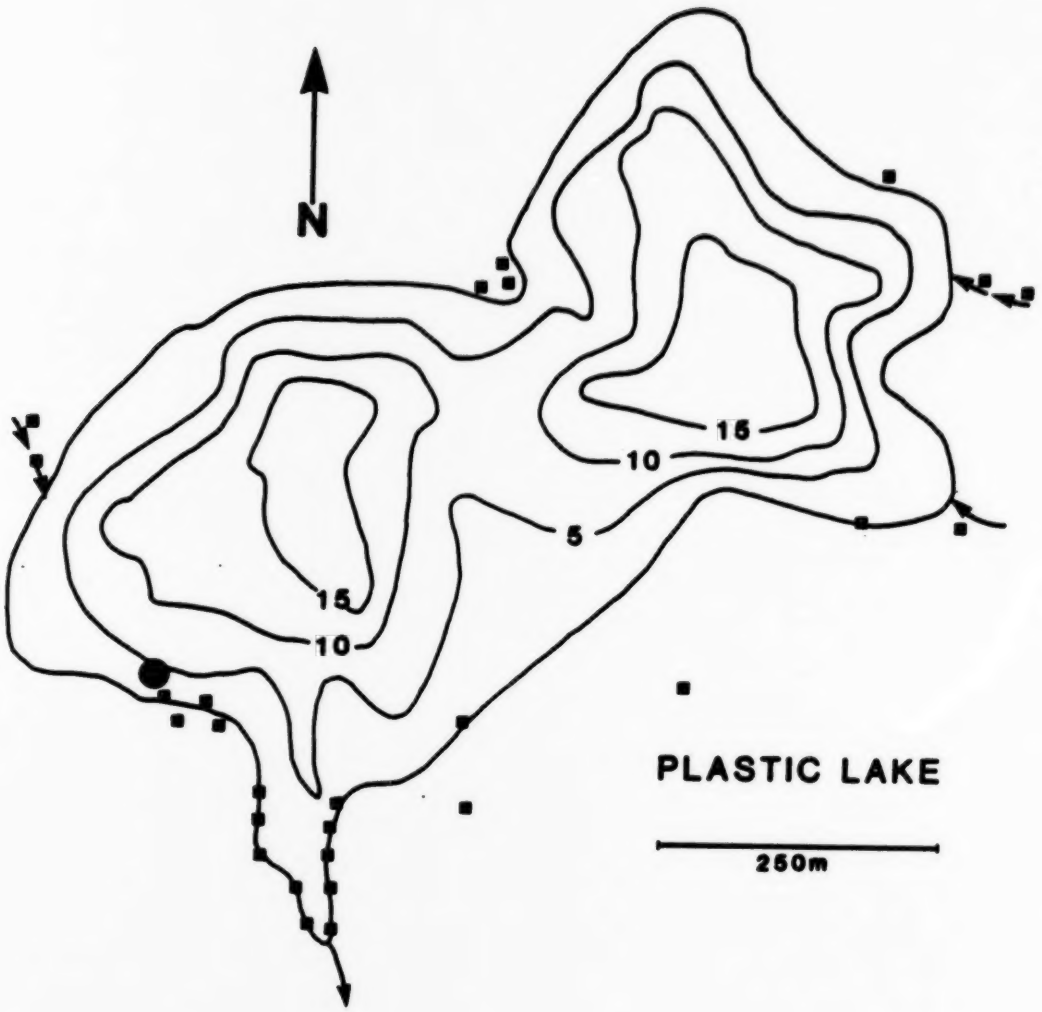

Figure 4

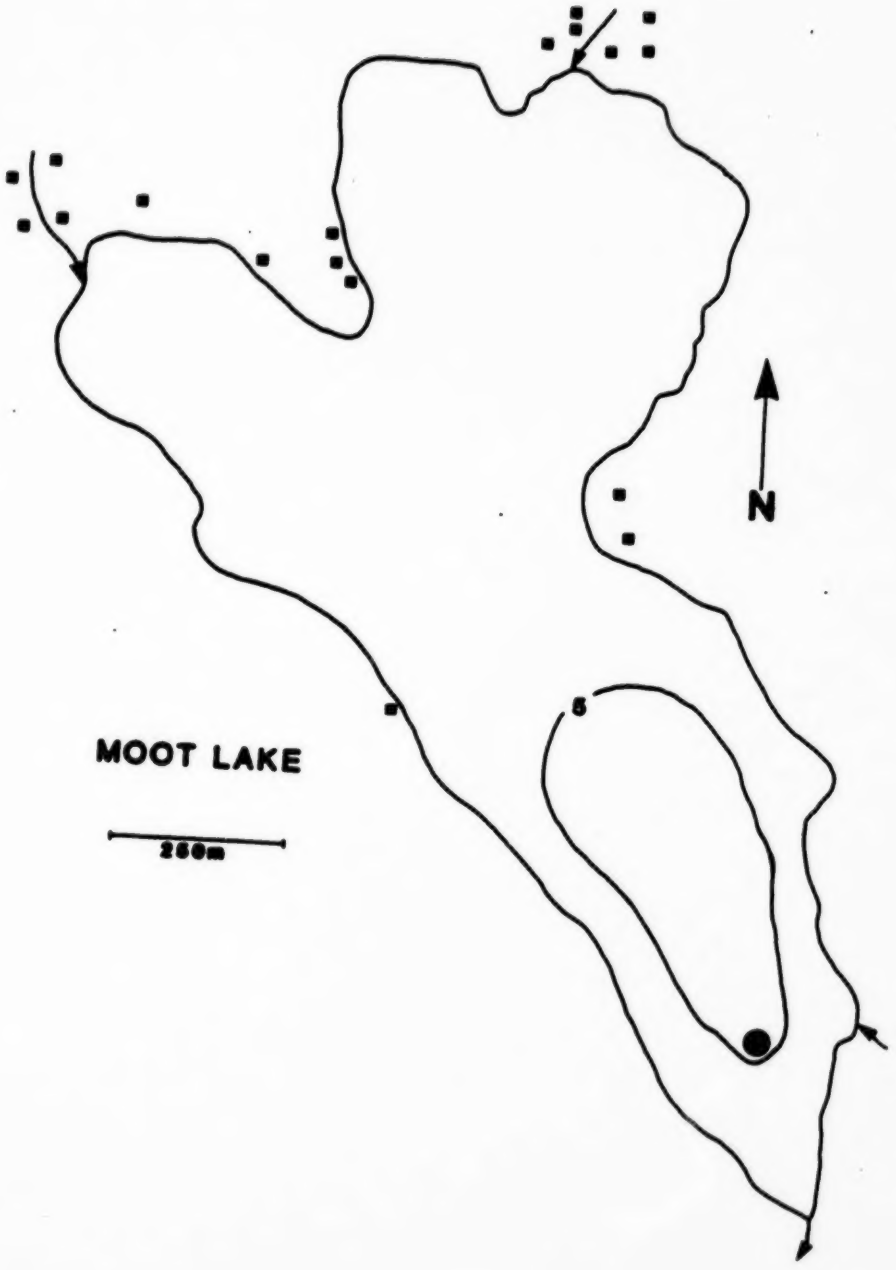

Figure 5

Crosson Lake

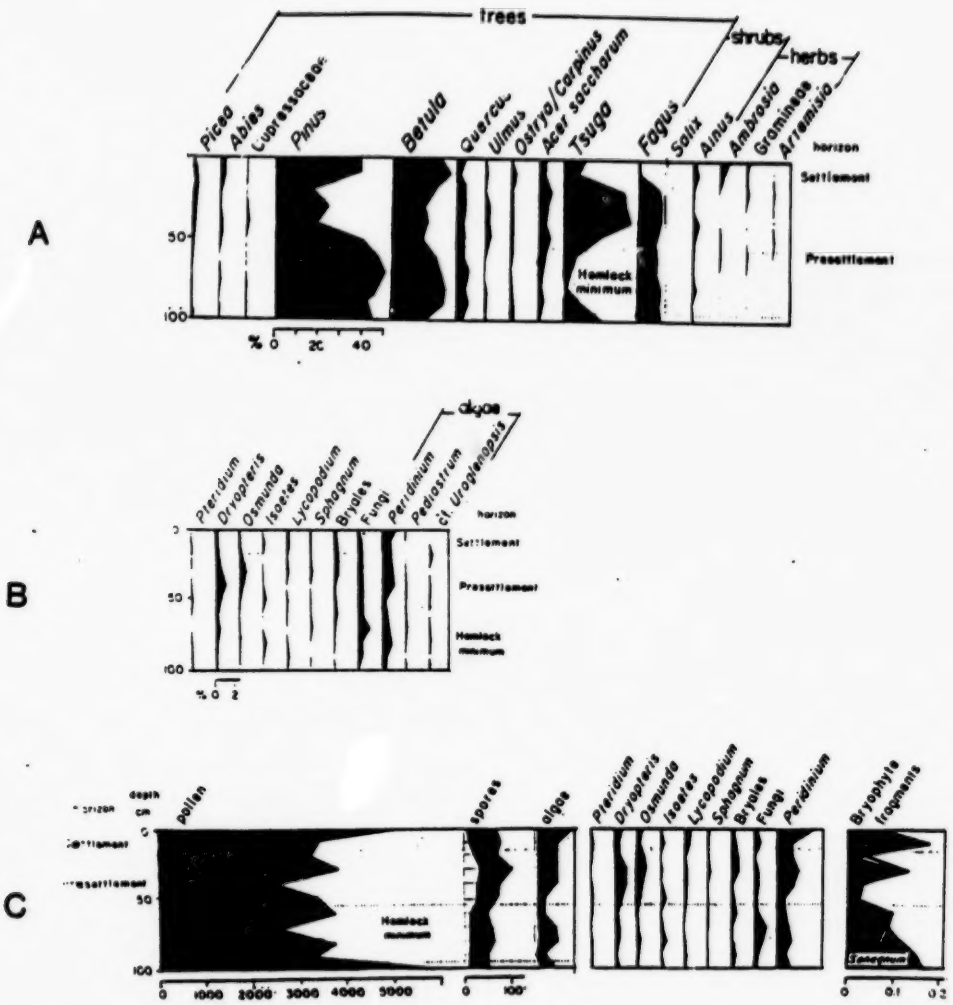

Figure 6

Gullfeather Lake

Figure 7

Moot Lake

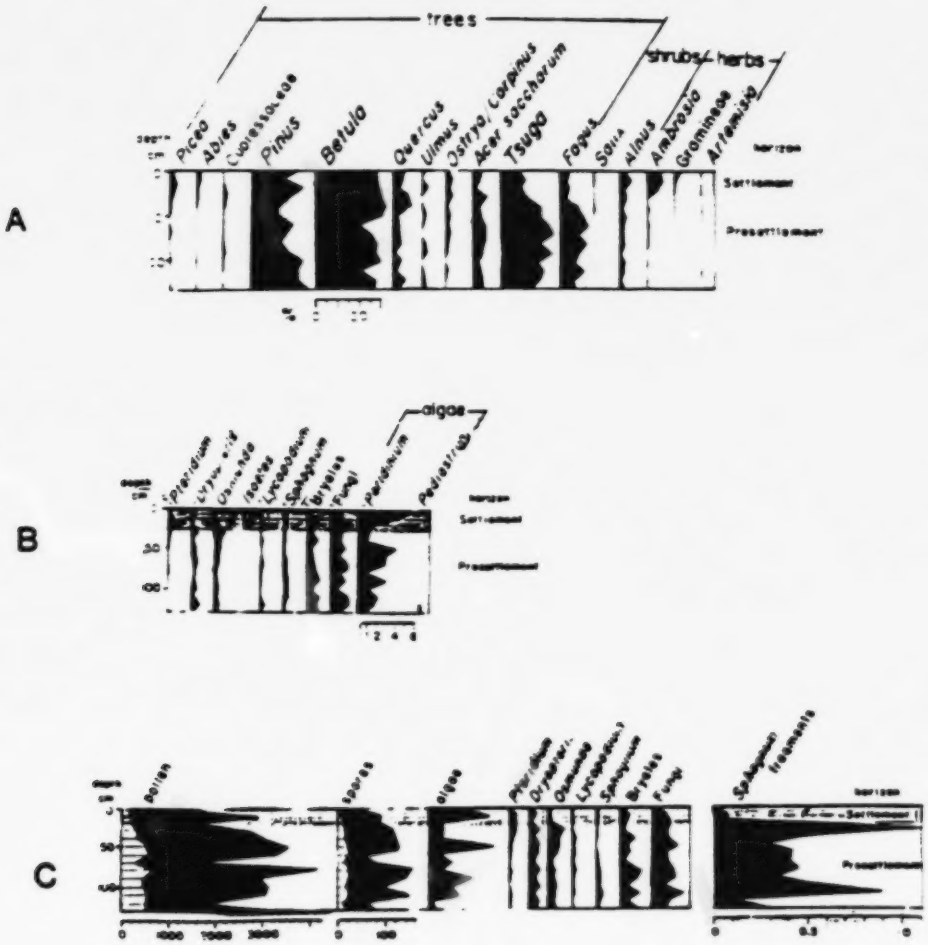

Figure 8

Plastic Lake